

PREDATORY INTERACTIONS AND NICHE OVERLAP BETWEEN MAKO SHARK, *ISURUS OXYRINCHUS*, AND JUMBO SQUID, *DOSIDICUS GIGAS*, IN THE CALIFORNIA CURRENT

RUSS VETTER, SUZANNE KOHIN, ANTONELLA PRETI, SAM MCCLATCHIE AND HEIDI DEWAR

NOAA Fisheries/Southwest Fisheries Science Center
8604 La Jolla Shores Drive
La Jolla, California 92037-1508

ABSTRACT

Recent scientific and anecdotal observations have documented a range expansion of jumbo squid, *Dosidicus gigas*, into the Southern California Bight (SCB) and northward in the California Current Large Marine Ecosystem. The increase in squid abundance at higher latitudes has generated hypotheses concerning the ecosystem changes that may have permitted this expansion. Top-down explanations suggest that overharvest of higher trophic level species such as tunas and billfishes creates a trophic cascade that increases survivorship of jumbo squid. Bottom-up explanations suggest that changes in ocean climate, including temperature and hypoxia, may favor an expanded range for jumbo squid. Here we present information on: (1) predatory interactions between the mako shark and jumbo squid in the SCB, (2) vertical niche of mako sharks and potential for a hypoxic refuge for jumbo squid, and (3) changes in the oxygen minimum zone (OMZ) and trends in epi- and mesopelagic prey. Mako sharks examined during the 2006 and 2007 NOAA Fisheries Southwest Fisheries Science Center Juvenile Shark Longline Survey had a high incidence of scars inflicted by jumbo squid. Diet studies based on the California Drift Gillnet Fishery, 2002–07 indicate that jumbo squid accounted for a substantial portion of the mako diet. Bioenergetic calculations suggest that the average 18 kg mako taken in the fishery would need 56–113 kg of squid to meet its annual dietary requirements. The high-resolution diel activity records of two representative animals indicate makos remained near the surface at night and were able to exploit the water column from the surface to a maximum depth of 300 m during the day. The maximum depth of dives corresponded to oxygen concentrations as low as 1.25 ml/L. Previous studies indicate that jumbo squid inhabit a depth range from the surface to the upper bounds of the OMZ where oxygen concentration is 0.5 ml/L or less. Jumbo squid in the SCB may have a deepwater refuge from mako sharks below 1.25 ml O₂/L, but are clearly available to mako during diel vertical migrations. Examination of the CalCOFI database for changes in oxygen content and larval fish counts over the previous 56 years indicates a shoaling of the OMZ and periodic

changes in abundance of epi- and mesopelagic prey species, but did not reveal a simple relationship between oxygen, prey availability, and range expansion. Better estimates of squid and mako population size and mako removal rates are needed to fully understand the impact of mako sharks on jumbo squid abundance.

INTRODUCTION

The jumbo squid, *Dosidicus gigas*, is a dominant mid-trophic link in the pelagic food webs of the Eastern Tropical Pacific (ETP; Olson and Young 2007). Recent studies originating in the Gulf of California (GOC), where jumbo squid are permanent residents, have described their age and growth, reproductive biology, and trophic niche (Markaida and Sosa-Nishizaki 2001, 2003; Markaida et al. 2004). Electronic tagging studies have provided new insights into the physical niche including horizontal and vertical movements, diel activity patterns, preferred temperatures, and a previously unappreciated tolerance of low-oxygen, mesopelagic habitats (Gilly et al. 2006). The mesopelagic oxygen minimum zone (OMZ) is a persistent feature of the ETP (Stramma et al. 2008) and extends northward throughout the California Current Large Marine Ecosystem (CCLME) usually at depths of 600 to 1000 m (Vetter and Lynn 1997; Chan et al. 2008). Two recent studies (Field et al. 2007; Zeidberg and Robison 2007) have reported a range extension of jumbo squid into the colder waters of the central California Current where they have been observed to a depth of 2000 m. Historically, the occurrence of the jumbo squid off California was restricted to periodic outbreaks, often associated with El Niño–Southern Oscillation (ENSO) events (Rodhouse, this volume). Interest by scientists, management agencies, and the general public has driven speculation on how the CCLME may be changing to allow this persistent northern range expansion. Proposed causes can be grouped into two categories: (1) top-down effects, such as removal of squid predators and competitors by fishing, which might increase jumbo squid survival and (2) bottom-up effects, such as changes in oceanography and prey fish abundance, that might increase favorable jumbo squid habitat. These speculations are not without controversy

(Watters et al. 2008; Zeidberg and Robison 2008) and are based on limited data. The Southern California Bight (SCB) has not been a focus of jumbo squid research but has been a focus of many long-term observing programs (e.g., California Cooperative Fisheries Investigations or CalCOFI). Records of potential jumbo squid predators (both fish and marine mammals), prey species, and baseline measurements of physical variables, such as oxygen saturation, are reasonably well known and may provide insights into the importance of top-down and bottom-up effects on jumbo squid abundance and persistence.

One apex predator that could affect jumbo squid in the SCB is the shortfin mako shark, *Isurus oxyrinchus* (Rafinesque 1810). The shortfin mako shark, herein referred to as mako shark, is a lamnid shark that inhabits temperate and subtropical seas worldwide (Compagno et al. 2005). Off the U.S. West Coast, the mako is a relatively abundant apex predator that utilizes the rich resources of the CCLME. In the U.S. West Coast Exclusive Economic Zone (EEZ) it is subject to both commercial and recreational fisheries (Cailliet and Bedford 1983; Hanan et al. 1993; Holts et al. 1998) and is managed under the Pacific Fishery Management Council's Highly Migratory Species Fisheries Management Plan as well as under state regulations (PFMC 2003). The SCB, between Point Conception and Cape Colonet, Baja California, Mexico, is said to be an important pupping and nursery area (O'Brien and Sunada 1994). As such, the majority of the U.S. West Coast commercial catch consists of neonates and juveniles of less than 145 cm fork length (FL) and estimated ages 0 to 3 (Hanan et al. 1993; O'Brien and Sunada 1994; PFMC 2003). Reproductively mature individuals are uncommon but seasonally targeted by the recreational fishery.

As is typical of members of the family Lamnidae, the mako shark is endothermic and has important physiological and biochemical adaptations that increase oxygen delivery, maintain high aerobic muscle performance and allow heat retention (Bernal et al. 2001). These adaptations are reflected in the mako's high metabolic rates (Graham et al. 1990; Sepulveda et al. 2007) resulting in a high caloric demand and daily ration (Stillwell and Kohler 1982). High aerobic activity may also limit foraging under low oxygen conditions. Although comprehensive diet studies of makos off the U.S. West Coast have not yet been conducted, the available data indicate that sub-adults here and elsewhere consume a diet primarily composed of fish and cephalopods with larger sharks consuming billfishes and marine mammals on occasion (Mearns et al. 1981; Stillwell and Kohler 1982; PFMC 2003).

To provide biological information for the management of mako sharks, the NOAA Fisheries Southwest Fisheries Science Center (SWFSC) is actively engaged

in the study of their migratory patterns, foraging activities, life-history characteristics, and population demographics. Primary sources of data include: (1) a long-standing research cruise, the Juvenile Shark Longline Survey (JSLS) conducted by the SWFSC, (2) fishery observers monitoring the California Drift Gillnet Fishery (CDGNF), and (3) the SWFSC CalCOFI survey that monitors ocean productivity and forage fishes. Through the JSLS, information on population biology and abundance is obtained and the survey provides a platform for biological sampling and traditional and electronic tagging studies. The CDGNF targets swordfish (*Xiphias gladius*), but mako sharks are an important and valuable incidental catch. Fishery observers aboard 20% of the trips monitor all catch and conduct biological sampling of stomachs, DNA, and gonads in support of studies on age, growth, reproduction, and diet. Both the survey and fishery focus on the SCB from Point Conception to the U.S.-Mexico border. The CalCOFI sampling program, in addition to shipboard measurements taken in conjunction with the JSLS and the CDGNF observer program, provides a time series of oceanographic data to help characterize the mako shark's habitat in the SCB.

In this paper we present recent observations on the mako shark-jumbo squid association and climate variables as they relate to the apparent increase and persistence of jumbo squid in the SCB. We discuss horizontal and vertical movements of mako sharks in the SCB as revealed by electronic tagging, the relationships between maximum dive depths and the thermal and oxygen profile of the mako shark and jumbo squid habitat, the extent of mako shark predation on jumbo squid, and the potential bioenergetic consequences of mako shark predation at the population and ecosystem levels. We also discuss changes in the oxygen structure of the SCB and changes in abundance of epi- and mesopelagic fishes as revealed by the CalCOFI oceanographic and ichthyoplankton time series. Our intent is to summarize recent observations within the SCB portion of the CCLME as they pertain to predatory interactions and niche overlap of mako shark and jumbo squid.

MATERIALS AND METHODS

JSLS Procedures and Visual Observations of Squid Scars

The JSLS has been conducted most summers since 1994 in the SCB aboard the NOAA RV *David Starr Jordan*. Sharks are caught during daylight hours using shallow-set longline gear baited with Pacific mackerel (*Scomber japonicus*). Two four-hour sets are conducted daily, each with two miles of stainless steel gear and 200 hooks set in the top 30 m of the water column. If a shark is caught, it is led to the stern of the vessel and restrained

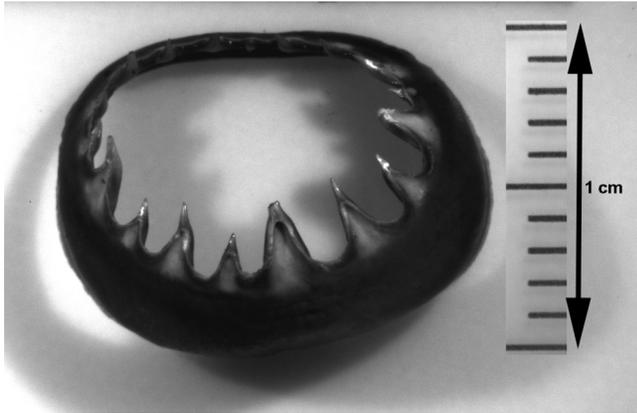


Figure 1. Toothed ring from the sucker of a feeding tentacle of *Dosidicus gigas* collected in the Southern California Bight during NOAA Fisheries Juvenile Shark Longline Survey.

in a specially designed cradle at the waterline. Depending on research needs (see below) different measurements and procedures may be performed, but at a minimum the hook is removed, total length or FL, sex, and species are recorded, the animal is tagged with conventional tags, and a DNA sample (fin clip) is obtained. Prior to release, each animal is evaluated for overall condition and assigned a score of poor, fair, good or excellent. During the condition evaluation there is time to observe scarring due to previous encounters with fishing gear, mating bites, or encounters with jumbo squid. Each sucker on the squid's arms and tentacles contains a ring of small grasping teeth (fig. 1) that produce characteristic marks (Barnes 1987; Nesis 1987).

Electronic Tagging

To study the migratory patterns of mako sharks in the CCLME, we have been deploying electronic tags during the JSLs as part of a SWFSC and Tagging of Pacific Pelagics (TOPP) collaborative project. Tags deployed include pop-off archival tags (PAT) which record water temperature, depth, and light level at one-minute intervals, and radio transmitting satellite-linked position tags (SPOT) which can be tracked through the Argos system (www.clsamerica.com) to provide horizontal movement information. The PAT (Wildlife Computers, Inc.) is anchored in the dorsal musculature near the first dorsal fin and the SPOT (Wildlife Computers, Inc.) is mounted high on the first dorsal fin so that it transmits whenever the fin breaks the surface of the water.

For this study, we focused on the behavior of two mako sharks that remained in the SCB during the fall months. For both sharks, we have detailed archival data due to the recovery of the PAT and accurate location estimates from the SPOT tags. The first shark, Mako1, was a 114 cm total length (TL) male tagged on 29 July 2004 with a model PAT3 tag and a model SPOT4 tag.

The second shark, Mako2, was a 191 cm TL male tagged on 30 June 2006 with a model PAT5 tag and a model SPOT5 tag. To examine their behaviors with respect to specific habitats within the SCB (i.e., nearshore vs. offshore), we identified archival data for which reliable Argos positions (location classes 1–3) indicated overlap in time and space with the CDGNF and the stomach sampling program.

Diet Analyses

Stomachs of mako sharks were collected during the 2002–06 fishing seasons by NOAA Fisheries observers aboard CDGNF vessels targeting swordfish. Sampling months were August through January and the majority (93%) of stomachs was collected within the SCB where the fishery is currently concentrated. The date, time and location of capture, shark FL and sex were recorded. Stomachs were frozen onboard and later transferred to the SWFSC La Jolla, California, laboratory where they were processed within six months.

Stomach contents were analyzed to the lowest possible taxon following the methods of Preti et al. (2001) using keys when necessary to identify species from hard parts (e.g., Clothier 1950; Iverson and Pinkas 1971). Data were analyzed for each season by prey taxa for relative measures of prey quantities (RMPQs) as follows: percent occurrence by number (%N), percent frequency of occurrence (%FO), and percent occurrence by weight (%W) of prey items. The value %N is the number of individuals of a specific taxon found in all stomachs divided by the total number of all prey found times 100; %FO is the number of stomachs containing prey of a specific taxon divided by the total number of stomachs containing prey times 100; %W is the total weight of all remains of a specific taxon divided by the total weight of all prey remains found times 100 (Hyslop 1980; Preti et al. 2001). Weight was the actual weight of the prey remains, not the estimated weight of prey at ingestion. Empty stomachs, slurry, and detritus were not used when calculating percentages. The values listed above were used to calculate the Geometric Index of Importance (GII). The GII, in its simplified form, is calculated as:

$$GII_j = \frac{\left(\sum_{i=1}^n V_i \right)_j}{\sqrt{n}}, \quad (1)$$

where GII_j = index value for the j -th prey category, V_i = the magnitude of the vector for the i -th RMPQ of the j -th prey category, and n = the number of RMPQs used in the analysis. In our study this is expressed as:

$$GII_j = (\%N_j + \%W_j + \%FO_j) / \sqrt{3}. \quad (2)$$

TABLE 1
Bioenergetic calculations used to convert metabolic estimates for an average 7 kg mako shark, *Isurus oxyrinchus*, to the amount of jumbo squid, *Dosidicus gigas*, consumed by mako sharks caught in the California Drift Gillnet Fishery.

Action	Process	Result	Reference
Energetic Cost			
Active metabolic rate	Mid-point between routine and max metabolic rate	443 mg O ₂ /kg/h for mean 7 kg shark	Sepulveda et al. 2007
Scale to 18 kg shark	Scaling exponent = 0.75	349 mg O ₂ /kg/h	Schmidt-Nielson 1997, Williams 1999
Convert mg O ₂ to J	1 mg O ₂ = 13.6 J	4752 J/kg/h	Jobling 1994
Add % lost to waste	Waste = 27%	6035 J/kg/h	Brett and Groves 1979
Convert J to kg squid	1 kg squid = 4.22*10 ⁻⁶ J	1.43*10 ⁻³ kg squid/kg/h	Cauffope and Heymans 2005
Convert to kg squid per shark per year	Modal shark = 18 kg	226 kg squid/y	NMFS observer data
Assume 25–50% of diet is squid		56–113 kg squid/shark/y	
Sharks Caught Annually			
Average Annual Landings 1981–2006		163,000 kg	PFMC 2007
Estimate number of sharks	Modal shark = 18 kg	9056 sharks	NMFS observer data
Squid Consumed			
Squid consumed by sharks caught	Assume 25–50% of diet	511–1021 mt squid/y	

We examined the sizes of squid consumed by sharks of different sizes. To calculate the mantle length (ML) of jumbo squid, upper rostral length (URL) was measured and the regression equation from Markaida and Sosa-Nishizaki (2003) was used:

$$ML = 129 + 30.5 \text{ URL}, \quad (3)$$

where the unit for ML and URL is mm.

Stomach contents were also examined during the JSLS from sharks which were collected for other ongoing biological studies. Because of the difference in sampling protocols, these stomachs were not included in the analysis to characterize mako diets. However, *D. gigas* remains were found in five stomachs of mako sharks of measured size (two samples from June 2004 and three from July 2007) and those beaks were measured and included in the relationship between prey size (squid mantle length as estimated from URL) and mako size.

Bioenergetic Estimates of Mako Metabolism and Ration

To calculate the energy requirements of the mako shark, standard energetic equations and equivalents were used (tab. 1). First, the active metabolic rate was estimated by taking the midpoint between the routine and maximum rates of oxygen consumption determined by Sepulveda et al. (2007). This resulted in a 29% increase above routine values. Similarly, in their study, Stillwell and Kohler (1982) added 25%–50% to adjust the routine metabolic estimate of mako sharks to an active metabolic estimate. Metabolic rate was estimated for a shark of modal weight taken in the CDGNF during the period 1990–2006 (NMFS observer data; SWFSC) using a scaling exponent of 0.75 (Schmidt-Nielsen 1997; Williams 1999). To convert mg O₂ to Joules (J), the

oxycalorific equivalent, 13.6 J = 1 mg O₂ (Jobling 1994), was used. This value was then adjusted for waste, assuming that 27% of ingested energy is lost (Brett and Groves 1979). To determine the mass of squid needed to provide the required energy to an average mako shark, J values were converted to mg of jumbo squid using 4.22 J = 1 mg (Cauffope and Heymans 2005). Finally, the overall energetic requirements of the population of mako sharks typically harvested in the CDGNF were calculated based on the annual fishery landings.

Methods of Analysis of Physical Oceanographic Data from CalCOFI

We used the Scripps Institution of Oceanography CalCOFI hydrographic database to compare the depth of the oxygen minimum layer between two five-year time periods (1951 to 1955 and 2001 to 2005). The survey domain was more extensive in the earlier period, so the comparison was only made for the SCB. We operationally defined the depth of the oxygen minimum layer as the depth of the 0.5 ml O₂/L isopleth (Mullins et al. 1985; Vetter et al. 1994). We averaged isopleth depths over July to December for all five years, and plotted the mean oxygen minimum layer depths as two isosurfaces for visual comparison.

Methods of Analysis of Ichthyoplankton Data from CalCOFI

Larval fish abundance can be used as an indicator of adult spawning biomass for many fish species (Lasker 1985; Ralston et al. 2003; Lo 2007). We obtained a CalCOFI time series (between 1951 and 2006) of larval fish data to examine trends in abundance of six species that are common prey in the diets of jumbo squid and mako sharks in the CCLME (Field et al. 2007; Preti

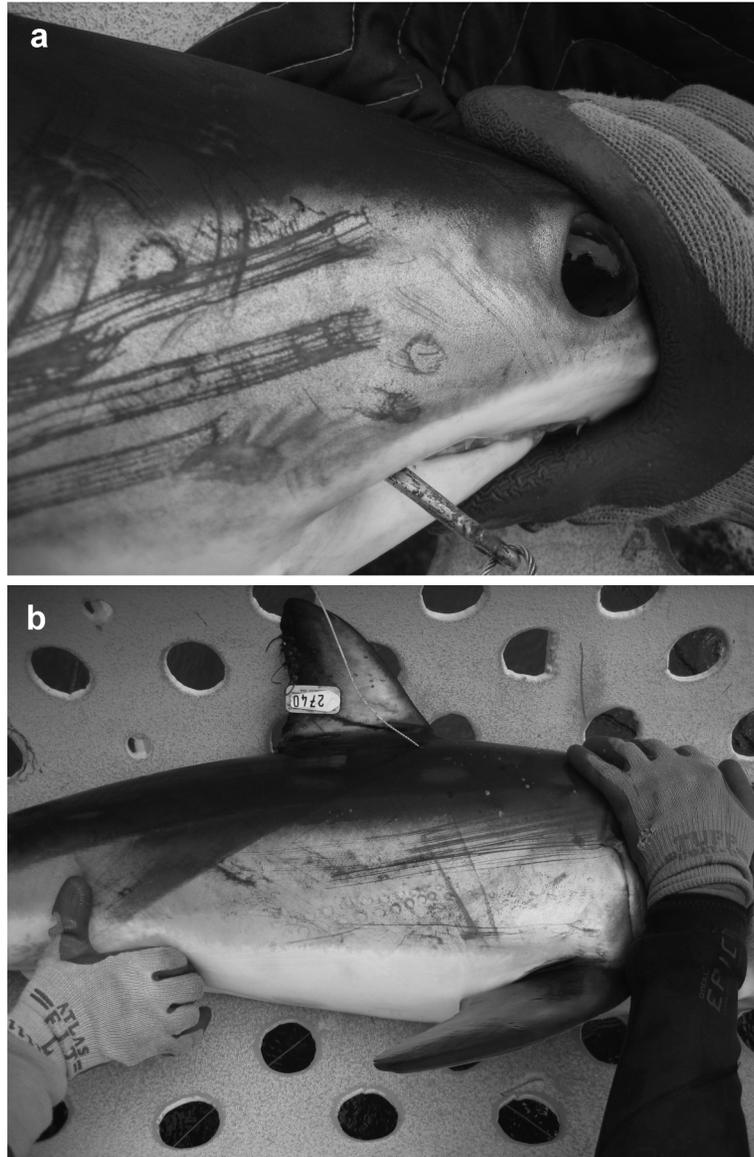


Figure 2. Shortfin mako sharks, *Isurus oxyrinchus*, in tagging cradle of RV *David Starr Jordan* during 2007 JSLs. (a) Scarring due to jumbo squid, *Dosidicus gigas*, sucker marks appear as rings of small incisions and as track marks that begin as a circular ring and continue as scratches across the skin of the animal. Marks are most prominent around the mouth of the mako. (b) Circular scarring and tracks on the midsection of a small mako.

et al., unpubl. data). They include northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), hake (*Merluccius productus*), shortbelly rockfish (*Sebastes jordani*), and two mesopelagic myctophid fishes, blue lanternfish (*Tarletonbeania crenularis*) and northern lampfish (*Stenobrachius leucopsarus*). Standardized larval abundances (number of larvae in $10/m^2$) were spatially averaged for each survey over all standard CalCOFI stations in the SCB for cruises during the spawning periods of each species (Moser et al. 2001). Larval abundances were scaled by subtracting the series mean and centered by dividing by the root mean square to make the time series comparable before plotting.

RESULTS

Visual Observations of Squid Scars on Mako Sharks

Observations made during the JSLs revealed that mako sharks are frequently covered with scars from jumbo squid. The scars appeared as a ring of small incisions (fig. 2a), or a series of parallel, linear scars, suggestive of the sucker and its teeth having been dragged along the skin (fig. 2b). Linear scars often begin with a circular mark on the shark's midsection and lead forward towards the mouth of the shark. The nature of the scars suggests that they were made as the shark ingested the jumbo

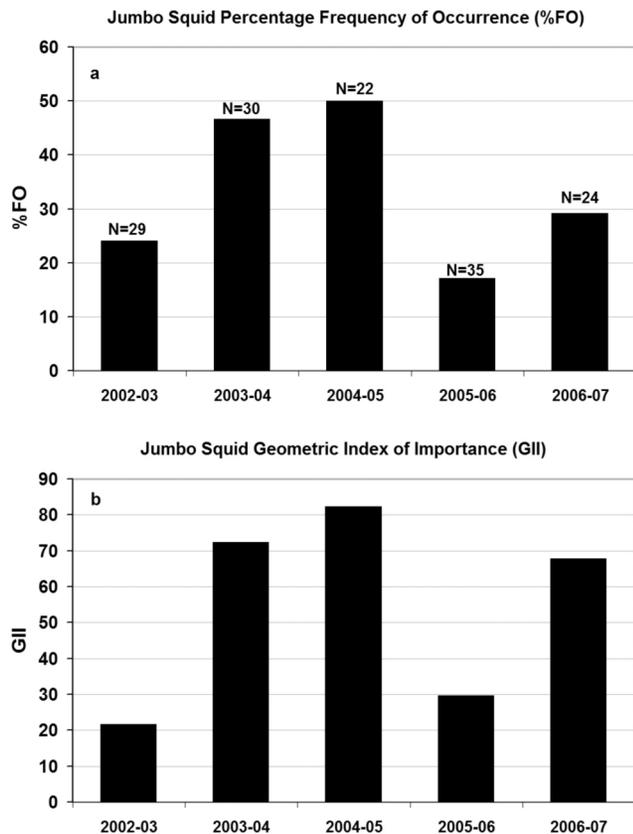


Figure 3. (a) Jumbo squid, *Dosidicus gigas*, percentage Frequency of Occurrence (%FO) in mako shark, *Isurus oxyrinchus*, stomachs by season ($N = 140$ stomachs with food). (b) Results of Geometric Index of Importance (GII) analyses for jumbo squid by season ($N = 140$ stomachs with food).

squid. Squid sucker marks have been observed on blue (*Prionace glauca*) and common thresher sharks (*Alopias vulpinus*), but the marks are faint and infrequent compared to those on makos. Although similar scars have occasionally been observed on makos during cruises prior to 2005, there is a general impression among the authors (Vetter and Kohin) that the frequency of occurrence and amount of scarring have increased and were particularly noticeable in 2006 and 2007.

Mako Shark Diet Studies

Analysis of 140 mako stomachs containing prey collected over five fishing seasons (2002–03 to 2006–07) reveals a high frequency of occurrence for jumbo squid in the stomachs of sharks captured in the CDGNF (fig. 3a). Shark FL ranged from 52 to 248 cm. Percent frequency of occurrence varied from 50% in 2004 to 17.1% in 2005. The mean %FO was 32.1%, indicating that over the five fishing seasons almost a third of the stomachs with prey contained jumbo squid.

The geometric index of importance, GII, which is a function not only of %FO, but also %N and %W, tends to vary more than the %FO alone. Nevertheless, the GII

clearly shows the importance of jumbo squid in the diet of makos caught in the CDGNF (fig. 3b). The GII can theoretically take on a maximum value of 173 in this analysis if there is only one prey taxon found in all stomachs. The GII for jumbo squid was always over 20 and had a maximum value of over 80 in 2004–05, indicating a high relative importance in the mako diet.

The stomach contents of animals that died during the JSLS were compared to those collected through the CDGNF observer program. Six mako stomachs examined from the 2004 and 2007 JSLS contained remains of jumbo squid, confirming their presence in the SCB during the summer months.

The derived mantle length of jumbo squid ingested by makos of different sizes is shown in Figure 4. While there is a positive correlation between the size of squid consumed and shark length ($r = 0.413$, $df = 66$, $p < 0.001$), even the smaller sharks consumed relatively large squid. The smallest mako sharks likely represent age 0–1 sharks and are not much larger than the published birth weights (60–70 cm TL; Compagno et al. 2005).

Mako Shark Horizontal Movements

We examined in detail the horizontal movements of two mako sharks tagged with electronic tags. Both sharks were tagged during the summer and spent up to five months in the SCB (fig. 5). Shark movements appeared directed at times when the animals transited rapidly, while at other times daily movements were much slower and the sharks remained in relatively focused areas for a week at a time or longer. When movements were restricted to focal areas offshore, horizontal movements averaged 13.9 km/day for Mako1 and 17.0 km/day for Mako2. When movements were restricted to a very small area in Santa Monica Bay, horizontal movements averaged 4.4 km/day for Mako1 and 2.0 km/day for Mako2. In contrast, during periods when the sharks demonstrated directed movements transiting between focal areas, rates of movements averaged 49.2 km/day for Mako1 and 45.6 km/day for Mako2. Based on their horizontal behaviors, we concluded that the sharks were likely foraging when in the focal areas offshore and within Santa Monica Bay (Le Boeuf et al. 2000; Tremblay et al. 2007). Thus, we examined the diving behavior and oceanographic conditions within these foraging areas to make inferences about the potential for mako and jumbo squid interactions.

Mako Shark Vertical Movements

In the offshore areas, both mako sharks spent greater than 99% of their time in the top 75 m of the water column (fig. 6a and c). Surface-water temperatures were lower in the offshore areas than near shore; however, even with occasional dives through the thermocline, 98%

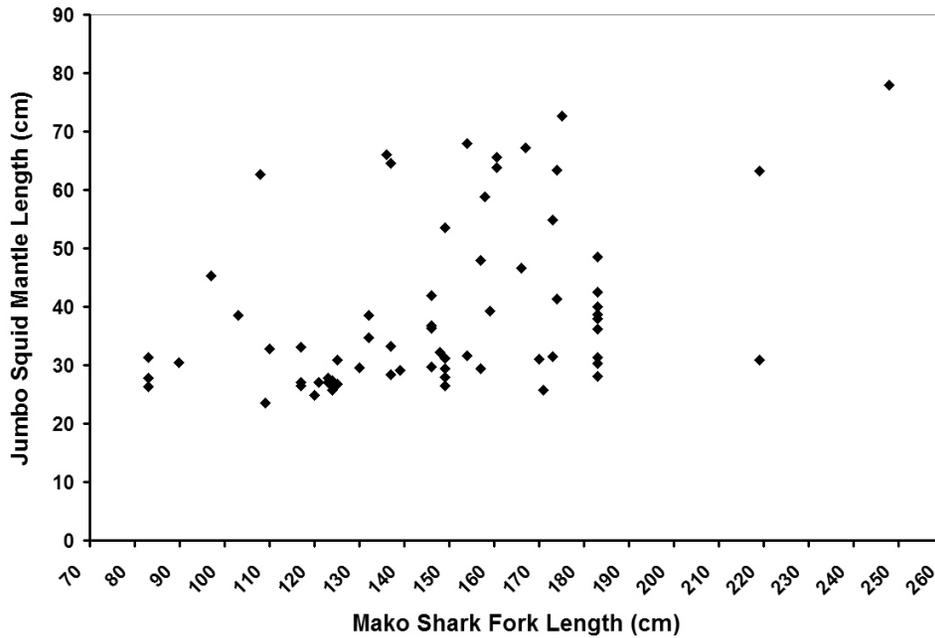


Figure 4. The relationship between mako shark, *Isurus oxyrinchus*, size (fork length in cm) and jumbo squid, *Dosidicus gigas*, size (estimated mantle length in cm) found in the stomachs of mako sharks.

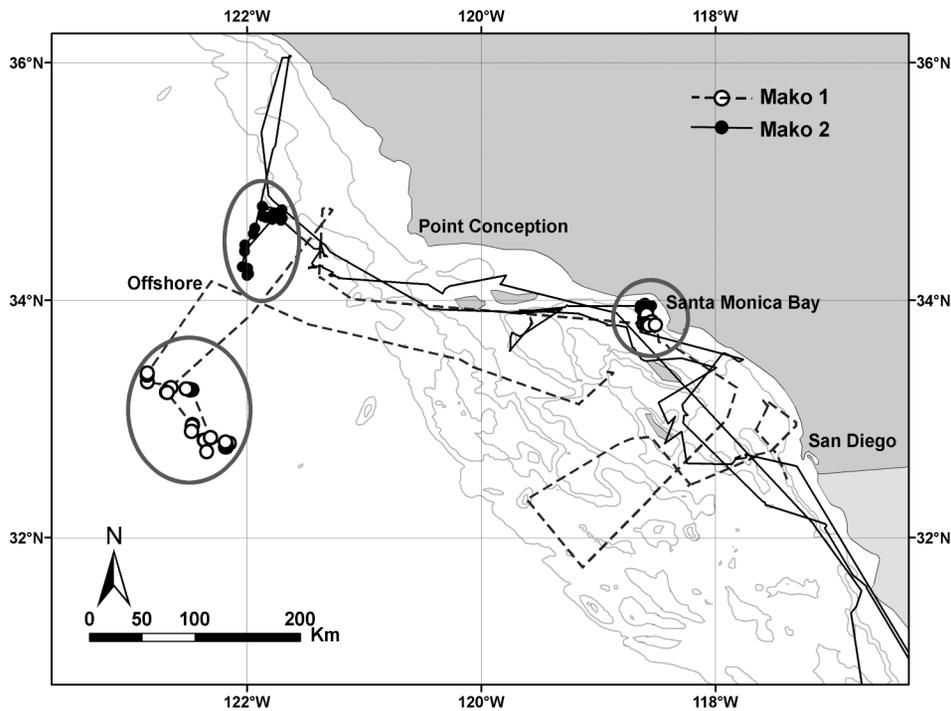


Figure 5. Horizontal movements of two mako sharks, *Isurus oxyrinchus*, in the SCB. Focal foraging areas where vertical behavior was examined include Santa Monica Bay and two areas offshore. Isobaths are 500, 1000, and 2000 m.

of their time was spent in waters warmer than 12°C. In contrast, in Santa Monica Bay, both sharks spent proportionately more time at depths exceeding 100 m (Mako1: 23.9%; Mako2: 18.5%; fig. 6b and d). Because of the greater diving activity, more time was also spent in water colder than 12°C (24.3% and 13.2%, respec-

tively). The greatest depth and coldest temperatures experienced by either shark in the focal areas was 324 m and 8.9°C. During excursions to depth in the Santa Monica Bay area, Mako1 experienced low dissolved oxygen levels. CalCOFI data for that time and area indicate that the 1.5 ml O₂/L isopleth is at approximately 245 m,

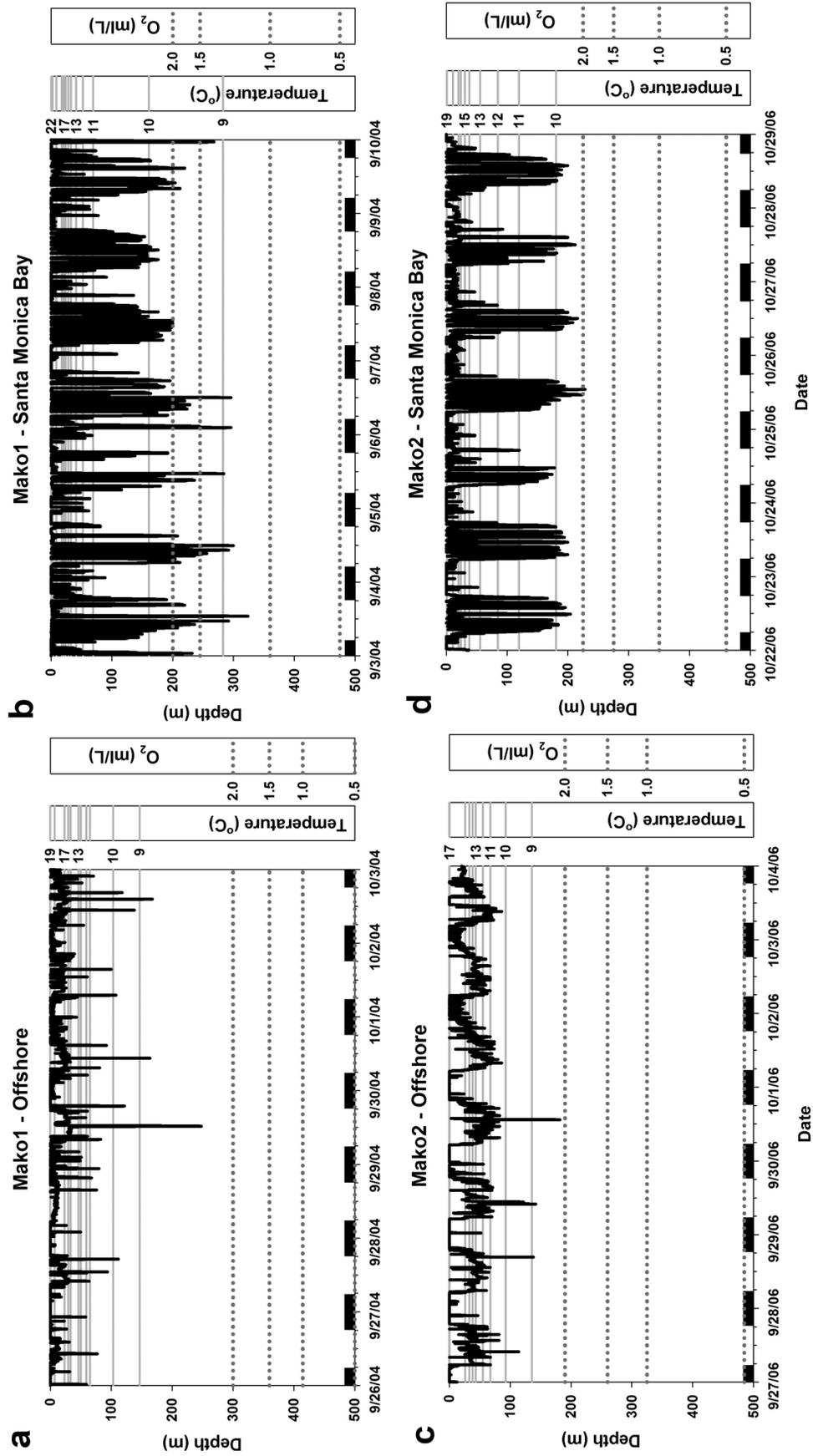


Figure 6. Vertical behavior of the two mako sharks, *Isurus oxyrinchus*, in the focal foraging areas. Black bars along the x axis indicate night periods.

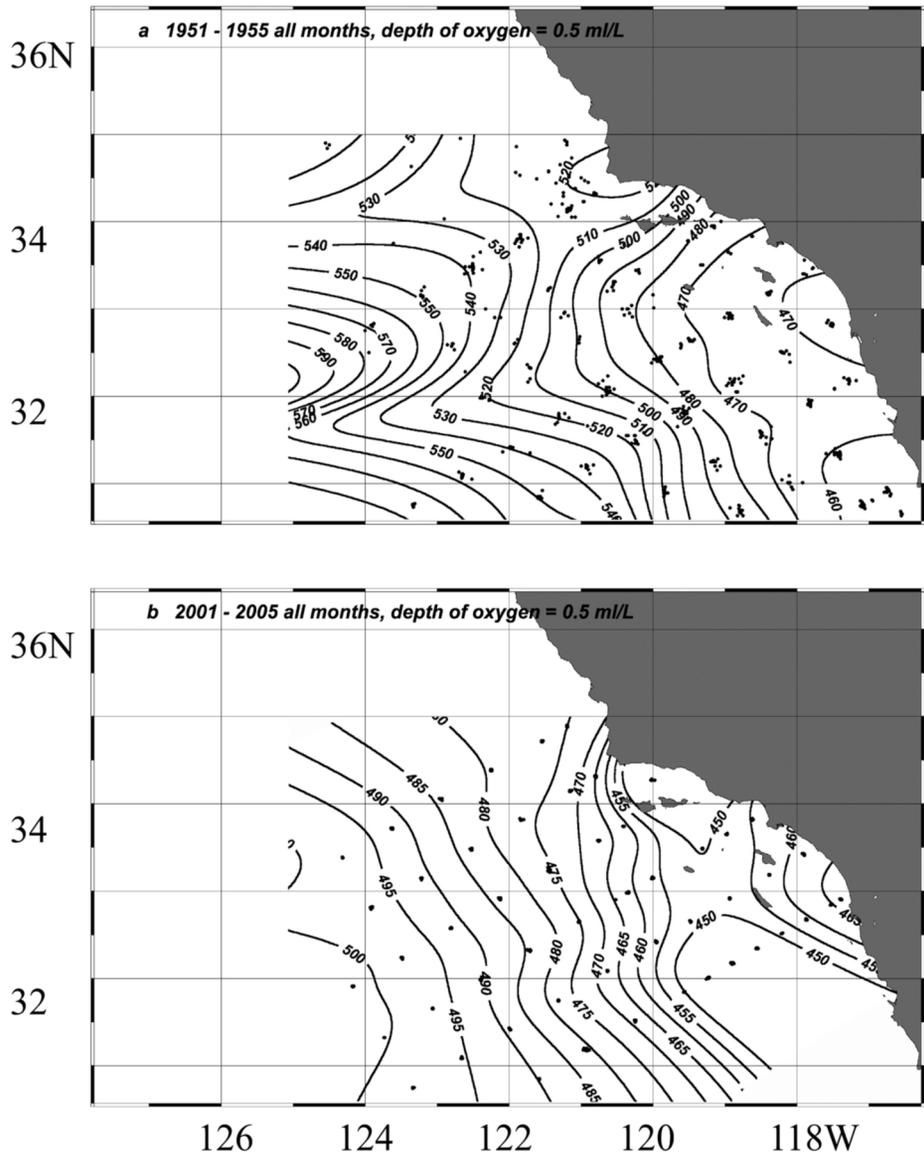


Figure 7. Comparison of the depth of the oxygen minimum layer (defined as 0.5 ml O₂/L concentration) between (a) 1951–55 and (b) 2001–05 in the Southern California Bight. Stations sampled in all of these years are shown as black dots.

TABLE 2
Comparison of ranked frequency of occurrence in the diet of jumbo squid, *Dosidicus gigas*, in the CCLME (Table 2 in Field et al. 2007) compared to the ranked abundance of fish larvae as they occur in the CalCOFI ichthyoplankton data (1951–98). Rankings are based on the 301 most common larval fish taxa identified to the lowest taxonomic unit (Table 4 in CalCOFI Atlas 34, Moser et al. 2001).

Common Name	Scientific name	Rank in Jumbo Squid Diet	Rank of Fish Prey Only	CalCOFI Larval Abundance Rank
Pacific hake	<i>Merluccius productus</i>	1	1	2
northern lampfish	<i>Stenobrachius leucopsarus</i>	2	2	6
northern anchovy	<i>Engraulis mordax</i>	3	3	1
blue lanternfish	<i>Tarletonbeania crenularis</i>	4	4	18
Pacific sardine	<i>Sardinops sagax</i>	5	5	7
shortbelly rockfish	<i>Sebastes jordani</i>	7	6	9
California headlightfish	<i>Diaphus theta</i>	8	7	29
broadfin lampfish	<i>Nannobranchium ritteri</i>	10	8	17
rockfish spp.	<i>Sebastes</i> spp.	11	9	4
California lanternfish	<i>Symbolophorus californiensis</i>	14	10	23

below which the shark dove on nine occasions. The longest excursion to depths greater than 245 m and with O_2 at levels less than 1.5 ml O_2/L was 19 minutes. Overall, the two mako sharks rarely encountered O_2 levels below 2 ml/L. For both sharks, there was a diel pattern of activity which was particularly pronounced in the Santa Monica Bay area; more time was spent making vertical excursions through the water column during the day, while the sharks generally remained within the upper mixed layer at night.

Bioenergetics and Trophic Considerations

Based on the modal size of makos taken in the CDGNF and the average total landings, the estimate of jumbo squid consumed by the makos harvested in the fishery is 511–1021 mt annually (tab. 1). The estimated size of the total population of makos in the CCLME is presently unknown.

Changes in the Depth of the Oxygen Minimum Zone

Visual comparison of the isosurfaces for the 0.5 ml O_2/L oxygen minimum layer over time reveals that the depth of the OMZ is shallower inshore compared with offshore and has shoaled in both regions over the last 50 years (fig. 7). The OMZ was about 30 to 70 m shallower offshore in 2001–05 compared to 1951–55. The depth of the OMZ inshore shoaled by about 20 m over the same period, which was a less marked change than offshore. One exception to this pattern was in the Santa Barbara Basin where the OMZ was 70 m shallower in 2001–05 compared to 1951–55 (fig. 7). The pattern of the isopleths in both periods shows that the OMZ “intensification” has been driven from the south.

Trends in Prey Fish Abundance

Table 2 describes the relationship between the ten most common fish species reported from the stomachs of jumbo squid in the CCLME (Field et al. 2007) and the ranked abundance of fish larvae averaged over the time period 1954 to 1998 when constrained to the core sampling region of the survey, roughly the SCB. Spatially averaged trends in the abundance of larval fish in the SCB have been highly variable since 1951, but still provide an important indicator of changes in epi- and mesopelagic fish biomass. The species shown in Figure 8 are the six most important fish species in the diet of jumbo squid (Field et al. 2007). The anchovy, hake, and rockfish began to fluctuate and then decline in importance during 1985–90. Sardine began to decline a little later, in about 1998. The mesopelagic fishes *Tarletonbeania crenularis* and *Stenobrachius leucopsarus* have shown no consistent trends in spatially-averaged abundance since 1980.

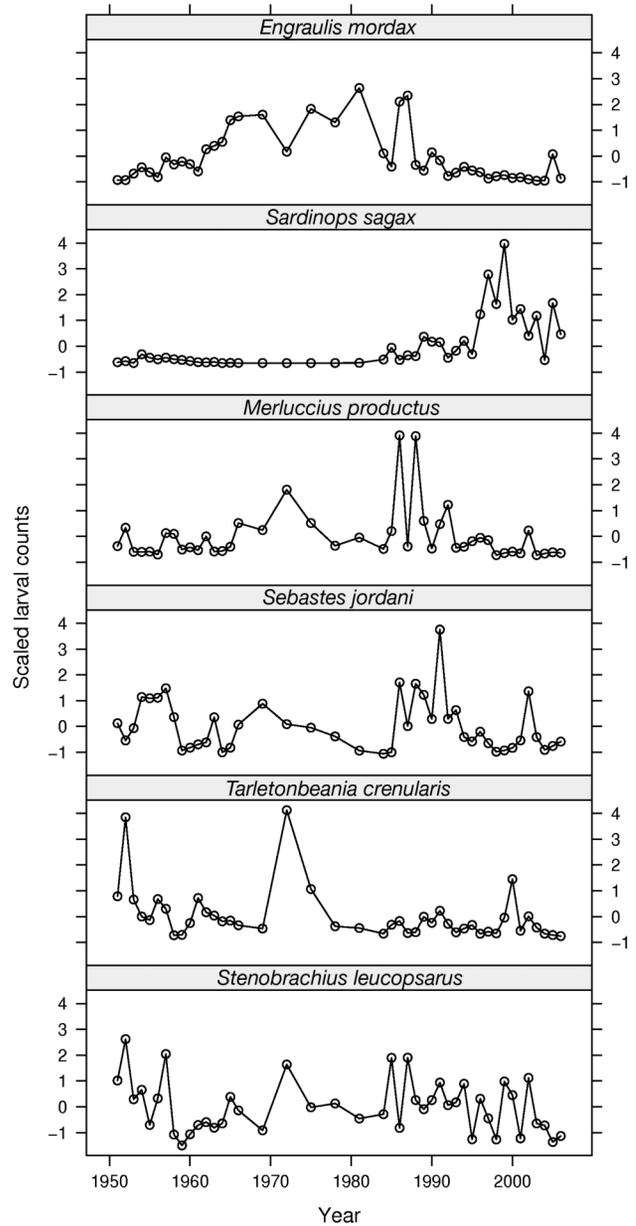


Figure 8. Time series of relative abundances of larval fish sampled with oblique bongo net tows in the Southern California Bight for the years 1950–2006. Data have been scaled and centered to make the series comparable.

DISCUSSION

The results will be discussed as they pertain to the leading hypotheses regarding jumbo squid range expansion: jumbo squid are expanding into the SCB due to top-down effects (a trophic cascade, sensu Myers et al. 2007) caused by reduction in top predators (Zeidberg and Robison 2007) or due to bottom-up effects, climate-linked changes in oceanographic conditions and associated biological changes in prey species (Field et al. 2007; Zeidberg and Robison 2007). To this we add a third mitigating factor: that shoaling of the OMZ may

provide a predation refuge even when highly aerobic predators such as mako sharks are abundant. None of these hypotheses are mutually exclusive.

Predation by Mako Sharks on Jumbo Squid

Like other widely distributed large pelagic predators, mako sharks probably utilize jumbo squid whenever they are abundant. Given the historic presence of jumbo squid off southern Baja and in the GOC where they are an important component of the diet of other large predators (Markaida and Hochberg 2005), it is likely that mako sharks have always consumed jumbo squid while in those waters. We suggest that jumbo squid are not novel prey for mako sharks, rather their persistent availability to mako sharks in the SCB is new. Juvenile mako sharks now have access to jumbo squid throughout their seasonal migration. A number of lines of evidence, photographic and diet, suggest an increase in predation on jumbo squid within the SCB in the last few years.

The JSLS has been conducted most summers since 1994; however, quantitative photographic documentation on the number and extent of squid scars is only now being implemented. Despite a lack of a systematic archive of photographs specifically designed to monitor the presence of scarring, hundreds of photographs from each cruise are available and, based on our observations of these, there is an increase in the extent of scarring on mako sharks in the past two years. The healed nature of many of the marks and the presence of jumbo squid beaks in the stomachs of mortalities sampled during the survey suggest that these encounters are predation events by the mako and not scavenging attacks by the squid occurring once the shark is hooked on the longline.

Additional insights are gained from other studies of mako shark stomach contents, such as the CDGNF stomach sampling program initiated in 2002. As such, if an increase in the occurrence of jumbo squid in the diet of mako sharks occurred as a consequence of the northward expansion of jumbo squid from 1998 to 2002, the stomach sampling program would not capture the change. Mako diet studies for the eastern North Pacific Ocean are scant; however, there is one published study of mako shark diets from the SCB based on five sharks sampled from the CDGNF in 1980 (Mearns et al. 1981) and no jumbo squid were present. In addition, a summary of mako diets based on published and unpublished observations prior to 2002 does not mention jumbo squid as important prey (PFMC 2003). No single diet index is perfect and little is known about differential rates of prey digestion and gut clearance between prey species and between tissue and beaks of jumbo squid. However, the high %FO and GII suggest that mako are deriving a substantial portion of their nutrition from jumbo squid.

To examine the energetic relationship between jumbo

squid and mako sharks, we estimated the potential for squid consumption by the locally harvested mako shark population. Based on standard energetic equations and using metabolic rate as a starting point, a mako of the average size taken in the CDGNF (18 kg) can consume 56–113 kg of squid per year, assuming that 25%–50% of their diet is squid. There are certainly limitations to these estimates due to the dearth of data available. One limitation is that the actual relative contribution of squid to the mako shark diet can not currently be estimated due to temporal and spatial limitations in sampling as well as a lack of data on the gut clearance time of beaks. The relative importance of jumbo squid in the mako diet has, however, likely increased in recent years due to the increased habitat overlap between the two species. A second limitation is that many of the metabolic conversions are based on other species and the metabolic rates themselves are extrapolated from a neonate shark. Nonetheless, the associated daily ration estimated in this study (3.4% of body mass per day) is similar to that reported by Stillwell and Kohler (1982) for mako sharks in the north-west Atlantic Ocean (3.2% at 19°C). As expected, this value is higher than for other shark species given the reported high metabolic rate of mako sharks and their regional endothermy (Graham et al. 1990; Sepulveda et al. 2007). For example, the estimated daily ration for blue sharks (*Prionace glauca*), which are not endothermic, is around 1% of body mass (Schindler et al. 2002).

To calculate a minimum estimate of the amount of jumbo squid consumed by mako sharks locally, we applied our energetic estimates to the population of sharks caught annually in the CDGNF. Using the average annual landings from 1982–2006 (163 mt; PFMC 2007), these mako sharks could consume 511 to 1021 mt of jumbo squid per year (tab. 1). The actual consumption of the local population of mako sharks is undoubtedly higher since only a fraction of the population is caught each year; however, abundance estimates are not available to extrapolate consumption to the population level. Other pelagic sharks such as bigeye thresher (*Alopias superciliosus*) and blue sharks are also important jumbo squid predators in the SCB (Preti et al., this volume). Furthermore, additional data are also needed on population estimates for jumbo squid in order to know what percentage of the population is affected by mako and other shark predation.

While overfishing of apex fish predators in the ETP may or may not have an indirect effect on jumbo squid demography and range expansion (Zeidberg and Robison 2007; Watters et al. 2008; Zeidberg and Robison 2008), commercial fishing mortalities in the U.S. West Coast EEZ for mako shark and other known jumbo squid predators, including blue shark, bigeye thresher shark, and swordfish, are much reduced in recent years due to

time-area closures and gear restrictions on longline and gillnet fishing. Most marine mammal predators, such as California sea lion (*Zalophus californianus*), Risso's dolphin (*Grampus griseus*), and sperm whale (*Physeter macrocephalus*), are fully protected and have increasing populations. We conclude that the removal of these top predators is an unproven explanation for the persistence of jumbo squid in the SCB.

Changes in Oxygen and Prey Fish Availability in the CalCOFI Time Series

Secular and episodic changes in temperature are well documented in the CCLME (Roemmich and McGowan 1995; Chavez et al. 2003; Field et al. 2006) and correlations between El Niño and northern range expansions of jumbo squid are well known (Rodhouse, this volume). The thermal tolerance of jumbo squid appears to be quite high and changes in temperature per se do not seem a reasonable explanation for northern range expansion. Jumbo squid can survive at 28°C in surface waters of the GOC (Gilly et al. 2006) and at 1.6°C at a depth of 2000 m in Monterey Bay (Zeidberg and Robison 2007). However, the physiological tolerance of jumbo squid to low oxygen conditions and the potential role of expansion of low oxygen waters in defining squid habitat has only recently been documented (Gilly et al. 2006). Studies to the north (Zeidberg and Robison 2007) and south (Gilly et al. 2006) suggest that jumbo squid probably routinely exploit a vertical niche from the surface to the upper portion of the OMZ. In Monterey Bay, the OMZ begins around 600 m and ends around 1100 m (Vetter et al. 1994; Vetter and Lynn 1997). In Monterey Bay, squid have most commonly been observed at 500 to 600 m, but a small number were observed below the OMZ at depths of 2000 m (Zeidberg and Robison 2007). In the GOC, the 0.5 ml O₂/L isopleth occurs at a depth of slightly less than 200 m in the region of jumbo squid tag deployments (Gilly et al. 2006). In both locations, long-term records of OMZ depth are incomplete or unavailable, so temporal correlations between changes in the OMZ and jumbo squid habitat are only beginning to be considered.

In the SCB, the depth of the OMZ varies from south to north and from inshore to offshore. Basins with limited circulation, such as the Santa Barbara Basin, have a shallower OMZ than the SCB as a whole. Analysis of the CalCOFI record presented here indicates there has been a shoaling in the depth of the OMZ between the initial period of CalCOFI sampling, 1951–55, and recent times, 2001–05. The Santa Barbara Basin and a region in the southern portion of the SCB have experienced the greatest shoaling of the OMZ, but changes have also occurred throughout the core of the CalCOFI pattern. Shoaling of the OMZ on the inner shelf has also

recently been reported off Oregon (Grantham et al. 2004; Chan et al. 2008). A more detailed examination of changes in the OMZ is underway, but preliminary examination of the temporal changes at key stations within the SCB does not suggest that there has been a dramatic change in the depth of the OMZ that temporally corresponds with either the 1998 pulse or the 2003 to present range expansion of jumbo squid (McClatchie, unpubl. data).

Within its core range, there have been numerous diet studies that clearly indicate that jumbo squid are opportunistic, generalist feeders that exploit a wide variety of epipelagic and mesopelagic fishes, cephalopods, and pelagic crustaceans (Wormuth 1976; Nesis 1983; Ehrhardt 1991; Nigmatullin et al. 2001; Markaida and Sosa-Nishizaki 2003; Markaida et al., this volume). In the GOC, jumbo squid diet contains a high incidence of myctophid fishes typical of the deep scattering layer (DSL; Markaida and Sosa-Nishizaki 2003) and the OMZ. It has been speculated that an increase in hypoxic habitat has led to an increase in mesopelagic fishes and subsequently jumbo squid have colonized and persisted in the SCB (Weiss¹).

To examine the potential for bottom-up dietary effects associated with the shoaling of the OMZ, we compared the squid's diet in the CCLME (Field et al. 2007) to changes in the abundance of epi- and mesopelagic fish species as reflected in the CalCOFI ichthyoplankton database. Given that the rankings of larval fish abundance are from more than 50 years of data and represent 301 of the most common fish taxa in the CalCOFI ichthyoplankton database, the correspondence between jumbo squid diet and fish abundance is striking and suggests that the jumbo squid in the SCB are generalists capable of consuming a wide variety of the most abundant epi- to mesopelagic fishes as they vertically migrate throughout the day and night. The ichthyoplankton abundance records for the six most common prey fishes break down into two epipelagic species (sardine and anchovy), two midwater generalists (hake and shortbelly rockfish), and two midwater (or DSL-associated) specialists (northern lampfish and blue lanternfish). An examination of the standardized changes in abundance over the past 56 years shows a number of interesting patterns that in some cases reflect climate changes at ENSO or PDO (Pacific Decadal Oscillation) scales of variation, and in some cases reflect the added effects of fishing and recovery of Pacific sardine (Moser et al. 2001). As with the OMZ record, there was not a clear signal that suggests that an individual species or group of species has changed abundance in a way that coincides with the re-

¹K. R. Weiss. 2008. "Oxygen poor ocean zones are growing." Los Angeles Times. 2 May 2008.

cent range expansion of the jumbo squid. Further work needs to be done, but this cursory examination of the physical oceanography and prey fish abundances does not point to an anomaly that reflects, in a simple way, the timing of jumbo squid range expansion.

Vertical Niche Overlap of Mako and Jumbo Squid

Based on electronic tagging data from the present and previous studies (Holts and Bedford 1993; Klimley et al. 2002; Sepulveda et al. 2004), makos in the SCB primarily exist within the top 200 m of the water column and exhibit greater vertical activity during daytime hours. Sepulveda et al. (2004) identified feeding episodes by monitoring changes in visceral temperature in free-ranging sharks. For animals tagged between June and November 2002, the majority of feeding events occurred during daylight hours at depths exceeding 100 m. Two other studies of makos tracked in the SCB revealed movements restricted to the top 50 m with no clear diel pattern (Holts and Bedford 1993; Klimley et al. 2002); however, tracking times were limited to 38 hours or less following capture and release. In the Atlantic Ocean, makos demonstrate similar diel behavior patterns of utilizing more of the water column during the day. Makos tracked in the vicinity of the Gulf Stream had a much greater depth range, reaching daytime depths of 400–550 m, although even at those depths water temperatures exceeded 12°C which is greater than temperatures encountered in the current study (Carey et al. 1981; Loefer et al. 2005). The difference in depth likely reflects the deeper thermocline in the Gulf Stream and possibly the larger size of sharks tracked.

For many highly aerobic fish, vertical distribution may be limited by oxygen availability as much as temperature (Randall 1970), and the concept of hypoxia-based niche compression has been developed to explain differences in the vertical distribution of tunas and billfishes in the Atlantic and Pacific Oceans (Prince and Goodyear 2006). Lethal O₂ thresholds based on laboratory studies of swimming performance in skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) were between 2.16 and 1.14 ml/L (Brill 1994). Prince and Goodyear (2006), based on previous studies (Ingham et al. 1977; Gooding et al. 1981; Bushnell and Brill 1991), considered 3.5 ml O₂/L to be a lower environmental limit for epipelagic billfishes and tunas in their study of hypoxia-based habitat compression. However, recent information from archival tagging indicates that many highly aerobic tuna and billfish species, such as bigeye tuna (*Thunnus obesus*), yellowfin tuna, and swordfish, are capable of occasional deep vertical excursions that can expose them to oxygen concentrations below 1.5 ml/L (Schaefer and Fuller 2002; Brill et al. 2005; Schaefer et al. 2007).

CalCOFI oceanographic data, overlapped with the mako tracks in this study, show that the mako sharks encountered O₂ levels near the thresholds proposed for tunas and billfishes. Mako1 dove to below the 1.5 ml O₂/L isopleth while foraging in Santa Monica Bay, yet never reached the same low O₂ levels while diving offshore where the OMZ was deeper (fig. 6a,b). The data collected to date on vertical movements reveal that mako sharks in the SCB appear to remain primarily above 300 m, 10°C, and 1.5 ml O₂/L (Bedford 1993; Holts and Klimley et al. 2002; Sepulveda et al. 2004; Kohin et al., unpubl. data). The vertical niche overlap between makos and jumbo squid remains to be determined pending archival tagging studies of squid in the SCB, but based on studies from Monterey Bay and the GOC it is likely that there is an area of high contact from the surface to about 300 m and perhaps a predation refuge between 300 m and the limits of hypoxia tolerance of the squid (conservatively the 0.5 ml O₂/L isopleth).

CONCLUSIONS

These results clearly indicate that mako sharks are utilizing jumbo squid as a major diet item in the CCLME. Relative to predators such as the sperm whale, tunas, and swordfish, pelagic sharks are somewhat overlooked and need to be better accounted for in the trophodynamics of jumbo squid and their impact on the CCLME. Better estimates of squid and squid predator abundances are clearly needed, but increased fishing restrictions, including time and area closures of the CDGNF due to leatherback turtle conservation, do not point to an increase in pelagic shark mortality within the U.S. West Coast EEZ. In addition, the population trends of most marine mammal predators are increasing or stable in the CCLME. At this time we conclude that top-down effects are not well supported. The idea that climate changes have produced favorable habitat may be true as there does appear to be an expansion of low oxygen equatorial waters in the SCB. However, it is unclear if jumbo squid favor low oxygen or simply tolerate it. Tolerance of low oxygen does appear to provide a partial refuge for jumbo squid from mako sharks. However, the diet of jumbo squid and their presence in the diet of mako sharks indicate that jumbo squid spend extensive periods of time in the oxygenated surface waters of the SCB. Finally, we were unable to find a simple temporal correlation between changes in oxygen, the abundances of the six most common squid prey fish, and the increase of jumbo squid in the SCB. A more detailed examination of water mass properties is in progress.

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